Using stable isotope analysis to study the migration and trophic ecology of eastern North Pacific white sharks (*Carcharadon carcharias*)

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Introduction

Background: White sharks are wide-ranging apex predators that utilize a large geographic area of the eastern Pacific Ocean. While they are primarily distributed along the coast during the fall and winter, they exhibit a regular offshore migration to oceanic habitats during the spring and summer, where they spend on average 7 – 8 months. The purpose of these migrations and their foraging behavior during them remains unclear. We used stable isotope analysis to provide insight into the trophic ecology and migratory behaviors of white sharks in the eastern North Pacific.

Stable isotope analysis: Stable isotope analysis (SIA) uses the stable isotope composition of elements in tissues to provide information on feeding and migration of an organism. This is possible because the stable isotope signature of an animal is directly related to that of its prey (you are what you eat) and the isotopic ratio shifts in a predictable manner as elements moves through successive trophic levels. The stable isotope signature of prey reflects that of the local food webs, and because isotope signatures of different food webs vary spatially due to differences in biogeochemical processes information about movements and foraging can be obtained. Stable isotope composition is expressed as δ values calculated using $\delta X = [(R^{sample}/R^{standard})-1)]*1000$, where $X = {}^{13}C$ or ${}^{15}N$, R = ratio of ${}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$, and the standards are Vienna Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen.

General questions:

1) Can the stable isotope composition of white shark tissue be used to demonstrate offshore foraging?
2) Can we use isotope values from potential prey items in different focal areas to derive plausible estimates of foraging in these habitats using a stable isotope mixing model?
3) Can we use an isotopic clocks to generate realistic estimates of when sharks return to coastal habitats?

Materials and Methods

White sharks were biopsied during tagging operations being conducted by the Tagging of Pacific Pelagics program (TOPP) in central California. Samples were collected using a biopsy probe attached to a tagging lance. Samples contained two tissues, dermis and white muscle.

SIA: Samples were lipid and urea extracted using petroleum ether and deionized water (respectively). Samples were analyzed at the UCSC Stable Isotope Laboratory, using an Elemental Analyzer coupled to an isotope ratio mass spectrometer (Delta XP-EA, Thermo-Finnagen IR-MS).

Characterization of focal areas: A literature review was used to obtain stable isotope composition for potential white shark prey in different focal areas: ***California***, ***Hawaii***, ***Pelagic*** (FIG 1**)**. The prey in these focal areas formed clusters that were distinct from each other.

Mixing model: Source (focal area) contribution to the different tissue types was examined using the Bayesian stable isotope mixing model MixSIR (Moore & Semmens 2008). Trophic enrichment factors (TEF) determined for leopard sharks (*Triakis semifasciata*, 3.7±0.4 SD for N, 1.7 ±0.5 for C, Kim 2010) were used.

Isotopic clock: We used the equation from Klassen et al. (2010) to estimate when sharks return to coastal habitats based on stable isotope composition. We used 3 different clocks based on different estimates of turnover rate: Logan & Lutcavage (2010) (sandbar shark), Carleton & Martinez del Rio (2005) (allometric bird), and Weidel et al. (2011) (allometric fish). Isotopic clock results were compared to time of return to coastal habitats observed by electronic tags (Pop-off archival satellite tags (PAT) and acoustic tags).

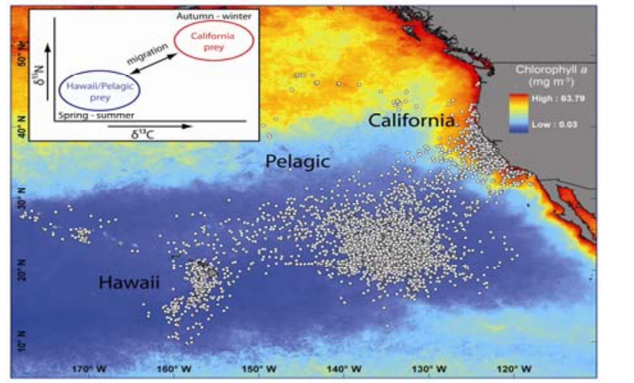

Fig. 1: White shark focal areas from Jorgensen et al. (2010). Mean chlorophyll-*a* concentrations (Aqua MODIS) for 2006 are shown to demonstrate productivity gradients which isotopic gradients generally follow. Inset shows conceptual diagram of seasonal migration between isotopically distinct regions.

Results

A total of 53 white sharks (35 ♂, 7 ♀, 11 U, TL 4.28±0.6) were biopsied between August and January (mainly early October) in 2006 - 2009, resulting in 48 dermal and 21 muscle samples.

Muscle and dermal tissues had distinct $\delta^{15}N$ and $\delta^{13}C$ values (muscle: $\delta^{13}C$ -15.5 ±0.5, $\delta^{15}N$ 18.3 ±0.8; dermis: $\delta^{13}C$ -12.8 ±0.5, $\delta^{15}N$ 19.3 ±0.9). Carbon and nitrogen isotope ratios decreased with size of shark, with smallest sharks being most enriched in ${}^{13}C$ and ${}^{15}N$ (FIG. 2).

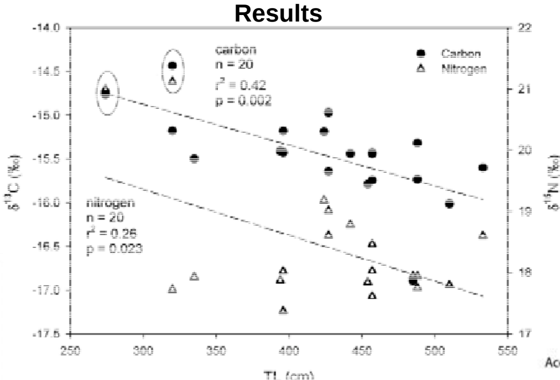

Fig. 2: Relationship between white shark length and $\delta^{13}C$ and δ^{15} N of muscle. The ellipses contain stable isotope values of two smallest sharks.

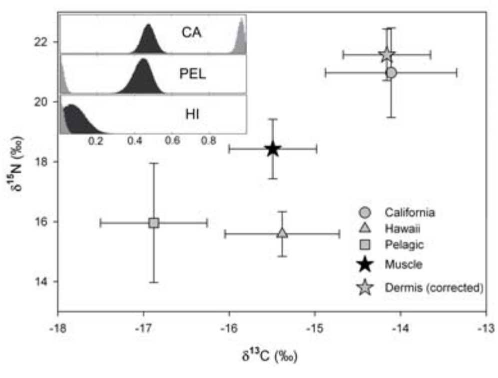

Fig. 3: Mean $\delta^{13}C$ and δ^{15} N values of parameters used in mixing model with inset showing mixing model results. Mixing model results show the posterior model estimates of focal area (California, Pelagic, Hawaii) contribution to muscle and dermis. Note that dermal values used in analysis were corrected to reflect muscle values

Mixing model outputs indicate muscle was a mixture of California prey (median 44%) and offshore pelagic prey (44%) with Hawaiian prey being a small component (8%). California was the primary source (94%) contributing to dermal tissue, suggesting this tissue may have a higher turnover rate and reflect recent foraging (FIG. 3).

Isotopic clocks estimated that white sharks returned to California on median dates of Aug 28 (sandbar shark rate), Aug 8 (allometric bird), and Jul 23 (allometric fish). These dates were concordant with electronic tag data which indicated sharks returned on a median date of Aug 11 (PAT tags) and Aug 30 (acoustic tags) (FIG. 4).

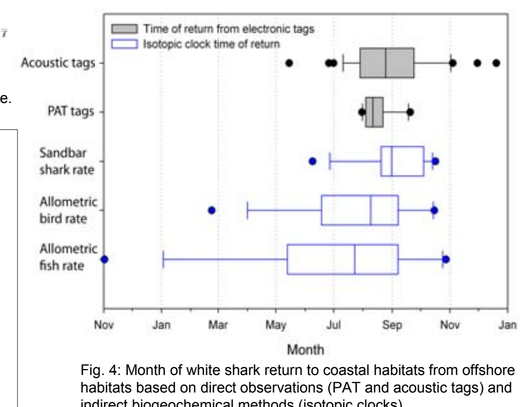

Fig. 4: Month of white shark return to coastal habitats from offshore habitats based on direct observations (PAT and acoustic tags) and indirect biogeochemical methods (isotopic clocks).

Conclusions

Our results demonstrate how SIA can provide insight into the trophic ecology, movements, and phenology of migratory behavior of white sharks, especially when coupled with electronic tagging data. These techniques could be used to monitor large scale migratory and trophic patterns in white sharks.

Results indicate that white sharks forage extensively during offshore periods. When offshore, sharks appear to forage more on prey in pelagic, oceanic habitats rather than nearshore Hawaiian waters. This is consistent with satellite tagging results, which suggest higher use of offshore, pelagic regions (white shark café) relative to the Hawaiian focal area.

Carbon and nitrogen isotope ratios decrease with size, possibly reflecting slower turnover in larger individuals. High stable isotope ratios in the smallest sharks suggests that white sharks may be residential along the coast until they reach size of first maturity (~300-400 cm TL). If true this may suggest a reproductive purpose to the offshore migrations

Isotopic clock estimates of time of return to California were generally consistent with electronic tag data though turnover rate greatly influenced results, showing the importance of using a robust estimate of turnover rate.

Dermis may be an new tissue to use for SIA, one with a relatively high turnover rate that can be easily and non-destructively sampled from elasmobranchs in the field to study recent foraging and movement.

Literature cited

Carleton & Martinez del Rio (2005) Oecologica 144: 226-232
Jorgensen et al. (2010). Proc. R. Soc. Biol. Sci. Ser. B. 277: 679-688
Kim (2010) Gaining insight into shark ecology using stable isotope analysis, PhD dissertation UCSC
Klassen et al. (2010), Funct. Ecol. 24: 796-804
Moore & Semmens (2008) Ecol Lett 11:470-480
Weidel et al. (2011) Can. J. Fish. Aquat. Sci. 68: 387-399.

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TOPP